PAST AND PRESENT DISTRIBUTION OF IGUANID LIZARDS [1]

(With 10 figures)

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ABSTRACT: The systematic diversity of the European iguanids is briefly reviewed. A new species, *Geiseltaliellus pradiguensis* sp.nov., is described from the Middle Eocene. The past distribution of iguanid lizards during the late Cretaceous and the Paleogene is examined and contrasted with their present distribution. These observations suggest that Iguanidae had a broad distribution during the late Mesozoic/ early Cenozoic and that, afterwards, iguanid lizards have withdrawn from Eurasia. Competition with other groups may have contributed to the extinction of Old World iguanid lizards. The fossil record shows that agamids did not play a central role in the extinction of iguanids. Mechanisms that affected the history of iguanids in Europe and Asia might be competitive interactions with lacertid lizards. Arguments for and against this hypothesis are examined. A test is carried out on the relative abundance of the iguanids and lacertids in Europe during the Eocene in order to reveal the potential role of competition.

Key words: Squamata. Iguanidae. Middle Eocene. France.

RESUMO: Distribuição passada e presente de lagartos iguanídeos.

A diversidade sistemática dos iguanídeos europeus é brevemente revisada. Uma nova espécie, *Geiseltaliellus pradiguensis* sp.nov., é descrita para o Eoceno Médio. A distribuição dos lagartos iguanídeos durante o Cretáceo e o Paleógeno é aqui examinada e contrastada com sua recente distribuição. As observações feitas sugerem que os Iguanidae tiveram uma ampla distribuição durante o Mesozóico Superior/Cenozóico Inferior e que, ulteriormente, os lagartos iguanídeos desapareceram da Eurásia. A competição com outros grupos pode ter contribuído para a extinção desses lagartos do Velho Mundo. O registro fóssil demonstra que os agamídeos não foram os responsáveis pela extinção dos iguanídeos. As interações competitivas com os lagartos lacertídeos devem ter sido os mecanismos que afetaram a história dos iguanídeos na Europa e na Ásia. Argumentos a favor e contra esta hipótese são examinados. É feito um teste sobre a abundância relativa dos iguanídeos e lacertídeos na Europa durante o Eoceno de forma a revelar o papel potencial da competição.

Palavras-chave: Squamata. Iguanidae. Eoceno Médio. França

INTRODUCTION

Today, iguanid lizards occur mainly in the Western Hemisphere but a few critical exceptions are registered in Madagascar and remote Pacific islands (Fiji and Tonga). The family has a wide ecological range in both tropical and temperate areas from extreme deserts to tropical rainforest interiors. Their fossil record is not very abundant but shows that the family has been in existence in Asia, North and South America, and possibly in Europe as early as the Cretaceous.

Generally, in the Old World, "iguanid niches" are occupied by agamid lizards (family Agamidae). The classic view (DARLINGTON, 1957) is that the iguanids have been replaced by the more advanced agamids on the Old World continents, notably in Africa. The recent discovery of fossil iguanids in Asia and Europe reinforce this suggestion. However, BLANC (1982) casts doubt on this hypothesis and he wrote: "we have difficulty explaining how the poorly diversified African agamids could have succeeded in totally supplanting the eventual iguanids. Their currently allopatric distributions appear to be more the result of general historical consequences than of competition."

KUHN (1944) named the first unquestionable european iguanid lizard, *Geiseltaliellus longicaudus*, together with the species *Capitolacerta dubia*. ESTES (1983) synonymized *Capitolacerta dubia* with *Geiseltaliellus longicaudus*. A comprehensive taxonomic revision of these lizards was published by HOFFSTETTER (1955), who rejected their assignment to the Iguanidae. However, ESTES (1983) demonstrated that the

specimens cannot be placed in any other family.

The time scale used for faunal analysis is that defined in SCHMIDT-KITTLER (1987) and BIOCHROM'97 (1997) (Tab.1).

Institutional Abbreviations: MNHN: Muséum national d'Histoire naturelle, Paris; USTL: Université des Sciences et Techniques du Languedoc.

SYSTEMATIC PALEONTOLOGY

EOCENE IGUANIDS

Four iguanid species are known in the European Eocene. The last European iguanids are recorded in the locality of Escamps (MP19), just before the "Grande Coupure", *i.e.*, the Eocene/Oligocene boundary. The traditional definition of the

Iguanidea is retained here (= non-acrodont iguanian), keeping in mind that the family could be paraphyletic (FROST & ETHERIDGE, 1989). In other words, the family is considered a metataxon, and neither monophyly nor paraphyly can be evidenced.

Order Squamata Oppel, 1811
Infraorder Iguania Cuvier, 1807
Family IGUANIDAE Gray, 1827

Geiseltaliellus Kuhn, 1944

Type-species – *Geiseltaliellus longicaudus* Kuhn, 1944

Known distribution – Early Eocene (MP7, Dormaal) to late Eocene (MP19, Escamps).
Germany, France, Belgium, ?Portugal.

TABLE 1. Stratigraphic positions of lacertilian localities in Europe. Subdivision of the European continental Eocene and Oligocene, based on mammalian standard levels for the Paleogene (MP), as proposed by SCHMIDT-KITTLER (1987) and BIOCHROM' 1997. These biostratigraphic intervals are correlated with the absolute scale (Ma) according to LEGENDRE & LÉVÊQUE (1997).

EPOCH	AGE - MARINE STAGES	MP	STANDARD-LEVELS	LOCALITIES
			France	Europe
EOCENE	-34	20		
		19	Rosières	Mormont-Entreroches
			Escamps	(Swiss)
	PRIABONIAN	18	Gousnat, Ste-Néboule	Osborne beds (England)
			La Débruge	
	-37	17	Perrière, Malpérié	
			Les Pradigues, Fons 1-7	Hordle Bed (England)
		16	Grisolles, Chéry-Chartreuve	
			Lavergne, Le Bretou, Robiac	
	-41	15		
	BARTONIAN			
		14	Lissieu	
		12-13	Saint-Maximin	Geiseltal oMK
	LUTETIAN			Geiseltal Umk (Germany)
		11		Geiseltal UK
	-49			Messel (Germany)
		10	Prémontré, Cuis	
			Grauves, Mas de Gimel	
	YPRESIAN	8-9	Sézanne, Condé-en-Brie	
			Avenay, Mutigny	
		7		Silveirinha (Portugal)
				Dormaal (Belgium)
PALEOC.		6	Berru, Cernay	
	THANETIAN			
		1-5	?Menat	Hainin (Belgium)
				Walbeck (Germany)
	-65			

Geiseltaliellus longicaudus Kuhn, 1944

Capitolacerta dubia KUHN, 1944: 364, Taf. 20.
Geiseltaliellus louisi AUGÉ, 1990: 114, fig.1.

Holotype – GM 4043, complete specimen, fig.1a-c, pl.19 *in* KUHN (1944).

Known distribution – Early Eocene (MP7) to Middle Eocene (MP16).
Germany, France, Belgium, ?Portugal.

Comments – *Geiseltaliellus longicaudus* (Figs.1-2) is characterized by having a long tail, three times the length of the body, and the parietal bears a sagittal crest. The teeth are slender, moderately heterodont: the first ten teeth are unicuspid and the following teeth are clearly triconodont, dentary tooth number is 20-25. Medially, the dentary shows a slender subdental shelf which has no sulcus dentalis. The ventral and dorsal borders of the dentary that define the narrow Meckelian canal are nearly contiguous anteriorly.

All records referred to the Iguanidae in Europe were rejected by HOFFSTETTER (1942, 1955). Nevertheless, the specimens cannot be placed in any other family: *Geiseltaliellus* has a heterodont dentition, its dentaries shows an interesting combination of high-crowned, tricuspid and highly pleurodont teeth, while lacking a sulcus dentalis (dental gutter). This combination of character states indicates that *Geiseltaliellus* is referrable to the family Iguanidae. The tricuspid condition in the Iguanidae is commonly characterized by having a large apical cusp and smaller anterior and posterior cusps. Tricuspid teeth are common in Teiidae, and also occur in some genera of Xantusiidae and Lacertidae. However, in the tricuspid teeth of teiids, the base of the tooth is often swollen and embedded in an important deposit of cementum. The tricuspid condition in the two genera of Xantusiidae is obviously different from that of iguanids: in xantusiids, the two side cusps are more lingually located than the central cusp. The majority of lacertid lizards bear bicuspid teeth, some have tricuspid dentition (*i.e.*, *Plesiolacerta lydekkeri*, from the French middle and late Eocene), but all lacertid lizards show a marked *sulcus dentalis* near the base of the teeth.

The fully preserved skeletons of *Geiseltaliellus* from Messel (MP11) near Darmstadt and the Geiseltal (MP12) pit near Halle (both in Germany), share a large number of morphological similarities with several species formerly (and erroneously) attributed to the Cordylidae.

Geiseltaliellus lamandini (Filhol, 1877)

Lacerta lamandini FILHOL, 1877: 489, 490, fig.421.
Pseudolacerta lamandini HOFFSTETTER, 1942: 239.

Holotype – incomplete right mandible, Old collections of the Phosphorites du Quercy, MNHN, QU 17739, fig.421 *in* FILHOL (1877).

Known distribution – End of the Middle Eocene (MP17, Malpérié) to the late Eocene (MP19, Escamps), France, Phosphorites du Quercy.

Comments – The teeth of *G. lamandini* are in general similar to those of *G. longicaudus*, differing in being more stoutly built. Medially, *G. lamandini* bears a clearly defined subdental shelf on the dentary, no definite *sulcus dentalis* can be recognized. The Meckelian canal is narrow, limited anteriorly by the nearly contiguous ventral and dorsal borders, as in *G. longicaudus*.

HOFFSTETTER (1942) described *Pseudolacerta lamandini* and *Pseudolacerta mucronata*, two Lacertilia from the Eocene of the Phosphorite du Quercy (France), as members of the family Cordylidae, opinion subsequently confirmed by AUGÉ (1987). However, this assignment cannot be maintained, owing to the morphology of the posterior part of the dentary and absence of a *sulcus dentalis* near the base of the teeth. In the holotype of *Pseudolacerta lamandini*, the posterior part of the dentary extends well under the coronoid, a position common to all iguanians, and very different from the morphology exposed in the Scincoidea (Scincidae + Cordylidae). Within the Scincoidea, the posterior part of the dentary does not reach the level of the middle point of the coronoid. Moreover, the posterior part of the dentary is deeply incised by the supraangular notch. Obviously, these features are absent from both *Pseudolacerta* and *Geiseltaliellus*. On these grounds, I have transferred the species *Pseudolacerta lamandini* to the genus *Geiseltaliellus*.

Geiseltaliellus pradiguensis sp.nov.

Holotype – Posterior part of a right maxilla having 14 well-preserved teeth, USTL, PRA 1221 (Fig.3).
Type-locality and range – Les Pradigues, Phosphorites du Quercy, France, end of the Middle Eocene (MP17).

Etymology – From the locality of Les Pradigues, France.

Material – Holotype (Fig.3); anterior part of a right maxilla, USTL, MAL 608, Malpérié (Fig.4) (Phosphorites du Quercy, France).

Known distribution – End of the Middle Eocene

(MP17), Phosphorites du Quercy, France.

Diagnosis – *Geiseltaliellus pradiguensis* sp.nov. is a middle Eocene iguanid distinguished from all other iguanid lizards by its teeth tricuspid, very slender, and tall. Only one-fifth of the tooth height projects beyond the level of the lateral parapet of the maxilla.

Description – The holotype consists of an incomplete right maxilla. The anterior part and the dorsal process of the maxilla are broken. Medially, above the tooth row, a deep, elongated notch (jugal groove) cuts into the posterior part of the supradental shelf. A large maxillary foramen opens in the supradental shelf, above the level of the fifteenth tooth (from the rear of the tooth row). The lateral surface of the jaw is smooth and bears a large lateral foramen.

The maxillary teeth are pleurodont, with the major part of each tooth attached to the lateral parapet of the jaw. The teeth are slender and very tall, slightly compressed under the crown. The tooth shafts are strongly compressed anteroposteriorly. Teeth are closely spaced. No *sulcus* separates the tooth row from the supradental parapet.

The tooth bases are attached close to the lingual border of the supradental shelf and they are not swollen; instead, several teeth have developed a median basal excavation for tooth replacement. The tooth crowns are markedly tricuspid, with a triangular central cusp flanked by two small lateral cusps.

A combination of characters of these maxillae strongly indicates their affiliation within iguanid lizards: tricuspid teeth, absence of a *sulcus* that separates the tooth bases from the supradental shelf; presence of an elongated jugal groove on the dorsal surface of the supradental shelf.

The two specimens are lumped together as *Geiseltaliellus pradiguensis* sp.nov. on the basis of their general resemblances in having tricuspid teeth, with only 20% of their height projecting beyond the parapet of the jaw. These two maxillae are referrable to *Geiseltaliellus* on the basis of their slender and high tooth shafts, their tooth crowns parallel-sided (*i.e.*, not flared) with a triangular central cusp and the deep, elongated notch on the dorsal surface of the supradental shelf. However, *G. pradiguensis* sp.nov. is clearly different from other species of *Geiseltaliellus,* primarily in having slender and high crowned teeth projecting only one/fifth of their height beyond the level of the lateral parapet of the jaw (as opposed to one/third in other species).

Geiseltaliellus sp.

Known distribution – Early Eocene (MP7), to the late Eocene (MP19).

Another, unnamed species is present at Grisolles (MP16) (Figs.5-6), northern France, and the last record of *Geiseltaliellus* is in the late Eocene of Escamps (MP19).

Pseudolacerta De Stefano, 1903

Type-species – *Pseudolacerta mucronata* (Filhol, 1877).

Pseudolacerta mucronata (Filhol, 1877)

Lacerta mucronata FILHOL, 1877: 489, fig.424. ZITTEL, 1893: 600.
Pseudolacerta mucronata HOFFSTETTER, 1942: 240.

Holotype – Dentary, certainly lost, MNHN, fig.424 *in* FILHOL (1877).

Known distribution – Middle Eocene (MP16) to the late Eocene (MP19). France, Phosphorites du Quercy.

Comments – Teeth strongly heterodont; the first teeth are unicuspid, posteriorly recurved with an slightly inflated base and a pointed apex. The following teeth are slender, tricuspid, and similar to the posterior teeth of *Geiseltaliellus*. The *sulcus dentalis* is lacking and the Meckelian canal is limited by curved borders. A combination of characters of the dentary indicates its affiliation within iguanid lizards: tricuspid teeth, absence of a *sulcus* that separates the tooth bases from the subdental shelf, absence of a dorsal ridge on the subdental shelf.

Pseudolacerta sp.

Known distribution – Middle and late Eocene (MP16-MP19), Phosphorites du Quercy, France.

Comments – A second species (still unamed) is known in the genus *Pseudolacerta*. Its dentary teeth are very similar to those of *P. mucronata*. *Pseudolacerta* sp. differs from *P. mucronata* by its narrow Meckelian canal limited by straight borders and its smaller size.

Cadurciguana Augé, 1987

Type-species (and only species known in the genus) – *Cadurciguana hoffstetteri* Augé, 1987

Cadurciguana hoffstetteri Augé, 1987

Holotype – Left dentary, USTL, ECC 2502, figs.1-3 *in* AUGÉ (1987).

Known distribution – Middle Eocene (MP16) to the end of the Late Eocene (MP19), France, Phosphorites du Quercy.

Comments – *Cadurciguana hoffstetteri* (Fig.7) shows strong evidence of iguanid affinities: total loss of the *sulcus dentalis*, faintly tricuspid teeth on the dentary, and greatly reduced splenial. Moreover, the frontals are fused and hourglass shaped, with the scar of the parietal foramen on the fronto-parietal border.
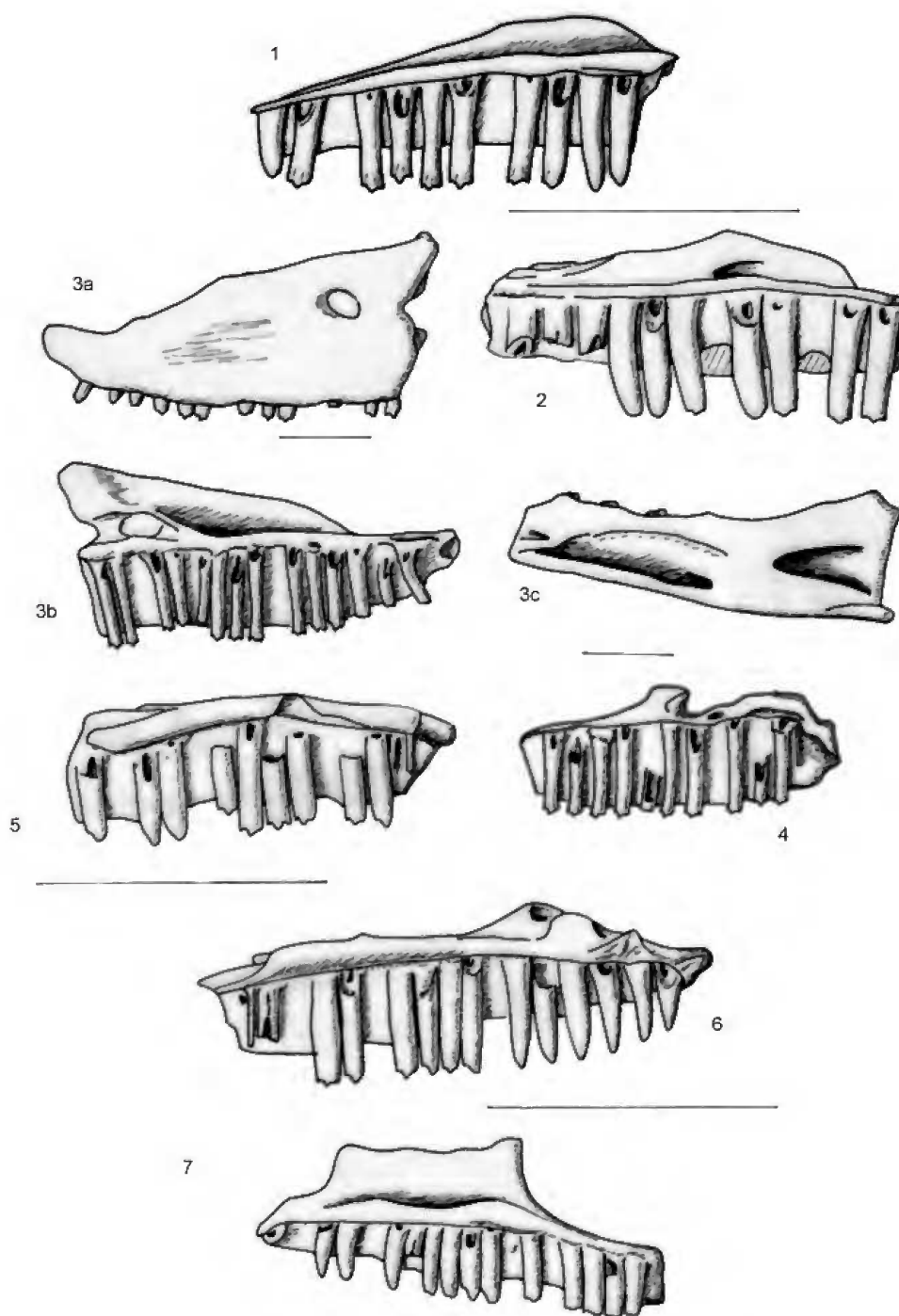
Geiseltaliellus longicaudus - fig.1- incomplete left maxilla, Prémontré, early Eocene (MP10), MNHN, medial view; fig.2- incomplete right maxilla, Dormaal, early Eocene (MP7), coll. E.Wille, medial view. *Geiseltaliellus pradiguensis* sp.nov. - fig.3- holotype, incomplete right maxilla, USTL, PRA 1221, Les Pradigues, middle Eocene (MP17); (a) labial view, (b) medial view, (c) dorsal view; fig.4- incomplete left maxilla, USTL, MAL 608, Malpérié, middle Eocene (MP17); medial view.; *Geiseltaliellus* sp. - fig.5- incomplete right maxilla, MNHN, Grisolles, middle Eocene (MP17); medial view; fig.6- incomplete left maxilla, MNHN, Grisolles, middle Eocene (MP17); medial view; fig.7- *Cadurciguana hoffstetteri*, incomplete right maxilla, MNHN, Le Bretou, middle Eocene (MP16); medial view. Scale bars: (1-2, 5-7) = 5mm, (3-4) = 2mm.

CRETACEOUS IGUANIDS

The discovery of late Cretaceous iguanids from Spain and France documents the earliest record for the Iguanidae in Europe. Two Campanian localities have yielded indeterminate iguanid lizards: Laño, in Spain (Basque Country) (RAGE, 1999), and Champ-Garimond in Southern France (SIGÉ *et al.*, 1997). The material is fragmentary but the maxilla and dentary bear pleurodont, flared, tricuspid teeth, strongly compressed labio-lingually. The resorption pits, when present, open at the medial side of the tooth base. Such teeth may belong to iguanid lizards, however, because of the fragmentary nature of the material, this assignment cannot be definitively ascertained.

These two early iguanids from the Upper Cretaceous of Europe provide fossil evidence supporting the interpretation of ETHERIDGE & DE QUEIROZ (1988) who regarded the tricuspid crown pattern as a primitive condition within iguanids.

DISTRIBUTION OF IGUANIDAE

Iguanids are a primarily American group of lizards but their distribution is clearly disjunct. Two iguanid genera exist in Madagascar and Grand Comore Island, *Chalarodon* and *Oplurus*. An iguanid (*Brachylophus*) has reached Fiji and Tonga in the Pacific, on which islands the genus is endemic. Fiji and Tonga also have giant extinct iguanids (PREGILL & DYE, 1989; WORTHY *et al.*, 1999). Such a puzzling distribution has been known as a "biogeographic enigma" or an "irritating problem" (BLANC, 1982).

Discoveries of late Cretaceous fossils of the group from Europe and the Gobi Desert (BORSUK- BIALYNICKA & ALIFANOV, 1991; GAO & HOU, 1995a, b; 1996) demonstrate the presence of iguanids in Europe and East Asia. The present pattern of distribution of iguanid lizards shows that they have withdrawn from Eurasia.

CARLQUIST's (1974) statement on the subject seems especially relevant here: "the best explanation seems to be that iguanas are a very ancient group of reptiles which have been extinguished on the Eurasian and African mainland". Two factors may have contributed to the extinction of Old World iguanid lizards: the Eocene-Oligocene climate deterioration and the competition with other groups. Here we examine the potential role of competition.

AGAMIDAE vs. IGUANIDAE

The development of better adapted families of lizards in the Old World could have caused the extinction of the Iguanidae in all areas where the families competed (AVERY & TANNER, 1971). Members of the family Agamidae are ecological equivalents for many iguanids and are widespread in the Old World. Agamidae have even been called "Old World counterparts of the New World iguanids" (*e.g.*, GOIN *et al.*, 1978). Some members of the two groups (Agamidae and Iguanidae) look alike and they do many similar things. Two of the most striking ecological equivalents are the Australian Thorny devil (*Moloch horridus*, Agamidae) and the North American horned lizard (*Phrynosoma platyrhinos*, Iguanidae), both of which exploit a diet of ants.

In the absence of direct information, the best evidence of competitive replacement between two groups of animals comes from their complementary distributions. Some 300 living species of agamids have an Old World distribution in southern Eurasia, Africa, and Australia. Nowhere in the world, except on Fiji, do iguanids and agamids live side by side, they have a complementary distribution. This complementary distribution is strongly suggestive of competitive interactions (DIAMOND, 1975). Hence, agamids may have caused the extinction of the Iguanidae where the two families overlapped.

The reality of competitive replacement should also be distinguishable in the fossil record: postulated competitors could have co-occurred in at least some part of their ranges (evidence for shared stratigraphic and geographic distributions) and the supposed better adapted group must replace or drive to extinction "inferior" group.

Agamid and iguanid lizards co-occurred in Europe and North America during the Eocene.

In Europe, agamid lizards made their first appearance in the early Eocene (MP7, locality of Dormaal), in the form of a single genus and species, *Tinosaurus europeocaenus* Augé & Smith, 1997. *Tinosaurus* becomes progressively less abundant during the early Eocene and its last record in Europe appears to be in the middle Eocene (MP13, DUFFAUD & RAGE, 1997). Thus, during the Eocene, the extinction of agamid lizards predated the disappearance of iguanids in Europe.

Agamids managed to enter North America during the Eocene, as demonstrated by the presence of the species *Tinosaurus stenodon* in the Middle

Eocene of Wyoming, but they were unable to persist on that continent after the Upper Eocene. During that time, iguanid lizards were well established in North America.

In both cases, the fossil record shows the persistence of iguanids while agamids became extinct, thus the expected pattern of replacement is not supported. Moreover, PIANKA (1986) and CLOUDSLEY-THOMPSON (1999) stated that the differences between the ecologies of most iguanid and agamid lizards that they studied are much more striking than are the similarities.

LACERTIDAE vs. IGUANIDAE

The radiation of Lacertidae during the Paleogene could be linked to the decline of the Iguanidae. Apparently, during the Cretaceous, only iguanid existed. Lacertidae arose during the Paleogene in Europe and radiated throughout the Eocene and the Oligocene. The iguanid lizards disappeared from Europe across the Eocene/Oligocene boundary and from Asia after the Oligocene.

On an other hand, lacertid and iguanid lizards display a perfect complementary distribution: they are entirely separated from each other in their geographic distribution today. The extant species of lacertids have an Old World distribution in Eurasia and Africa and they are absent from Madagascar and North and South America.

It is clear that lacertid and iguanid lizards were sympatric during part of their evolution in Eurasia. They have co-occurred during the Eocene in Europe and both families are known in the Asian fossil record. Does the fossil record confirm the hypothesis of competitive replacement (Fig.8)?

North and South America: iguanid lizards have been well established in North and South America since the Cretaceous. There is a purported Mesozoic record of an iguanian from the Upper Cretaceous of Brasil (*Pristiguana* Estes & Price, 1973) (ESTES & PRICE, 1973). Moreover APESTEGUIA *et al.* (2005) report an incomplete lizard frontal from the Cretaceous of Patagonia that could belong to an iguanid. Some iguanid taxa have been recovered from the late Cretaceous of Canada (*Cnephasaurus* and two unnamed genera, GAO & FOX, 1996). Extant lacertids are absent from the continent and no records of fossil lacertids are known.

Madagascar: lizards are the most speciose group of terrestrial vertebrates on the island of Madagascar, the extant lizard fauna includes chamaeleonids, iguanids, scincids, cordylids, and gekkonids. Typical mainland African forms (agamids, lacertids, varanids) are absent. Moreover, the lizard fossil record from Madagascar is nearly lacking (KRAUSE *et al.*, 2003).

Africa: Scincomorph lizards have been discovered in the Upper Jurassic of Africa (ZILS *et al.*, 1995; BROSCHINSKI, 1999), but true lacertids are not known in Africa before the Quaternary. Extant and fossil iguanids are apparently absent from Africa.
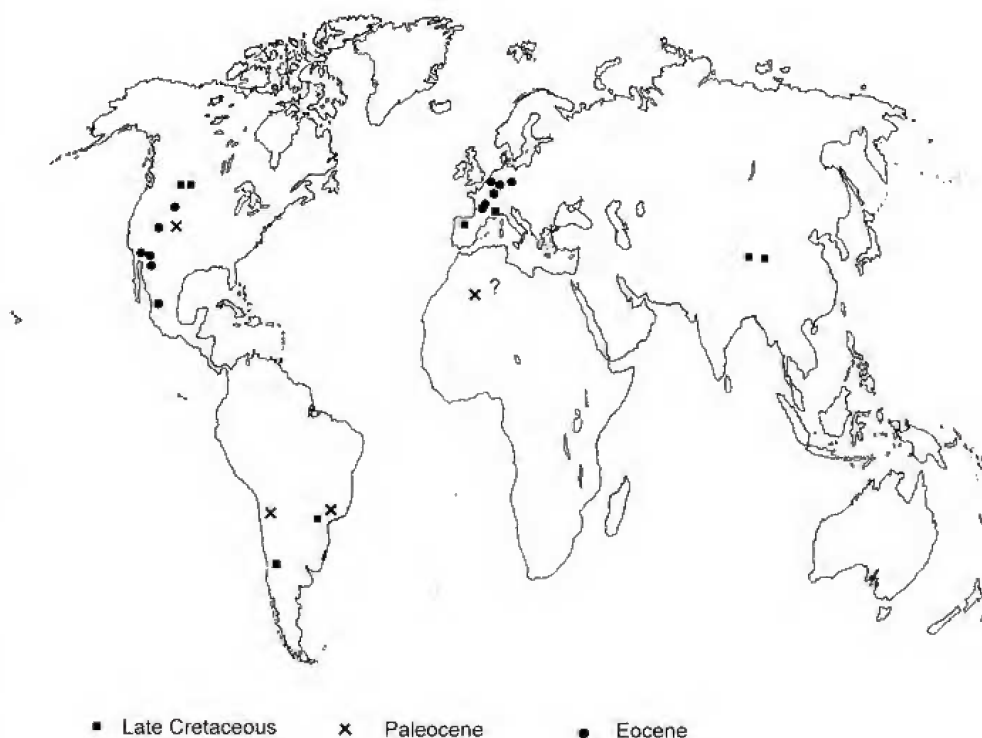

Fig.8- Distribution of fossil iguanid lizards.

However, some fragmentary dentaries from the Paleogene of Morocco have tricuspid teeth that suggest iguanids affinities. It must be added that the two specimens in hand are poorly preserved and their assignment is highly debatable.

Asia: the Mesozoic iguanid record of Asia has been recently improved. Early Cretaceous deposits in Central Asia and Mongolia have yielded indeterminate iguanians (Gao & Nessov, 1998), while a diversity of iguanid taxa has been recovered from the Campanian and Maastrichtian of Mongolia and China (Alifanov, 1996; Borsuk-Bialynicka & Alifanov, 1991; Gao & Hou, 1995a, b, 1996; Gao & Norell, 2000). Maybe iguanid lizards were still present in Asia during the Paleocene, their last occurrence on the continent appears to be from the Oligocene (Ckhikvadze *et al.*, 1983; Alifanov, 1993).

Alifanov (1993) suggests a long "cryptic" history of the Lacertidae during the late Cretaceous in Asia. However, in a personal communication, V. R. Alifanov states "In 1993, I published the preliminary information about the Cretaceous lacertids, but now I think it was an error. In any case I do not regard true lacertids as an Asiatic group in origination." Apparently, lacertid lizards made their first appearance in Asia during the late Paleogene (Oligocene?).

In Asia, the fossil record shows the persistence of lacertids while iguanids became extinct, supporting the expected pattern of replacement.

Europe: iguanid lizards are present during the entire Eocene in Europe. The last European iguanids are recorded in the locality of Escamps (MP19), just before the "Grande Coupure", *i.e.*, the Eocene/Oligocene boundary.

The locality of Hainin (Paleocene, MP1-5) could contain a lacertid fossil (Van Dyck, 1983). However, this record is not confirmed by Folie (2006). The first confirmed lacertid lizards has been yielded by the locality of Cernay (France), from the Upper Paleocene (Augé, 2005). Lacertid lizards are well-represented in the fossil record during the Eocene and the Oligocene in Europe. Only one genus, *Dormaalisaurus*, is known in the early Eocene of Dormaal, Belgium, but three genera are recorded from the late Eocene (*Plesiolacerta* and two new genera). *Succinilacerta succinea* (Böhme & Weitschat, 1998; Borsuk-Bialynicka *et al.*, 1999) is another small genus preserved in the Baltic amber (certainly middle Eocene).

To sum up, in Europe and Asia, the fossil record shows the persistence of lacertids while iguanids became extinct, supporting the expected pattern of replacement. Moreover, apparently lacertids have never reached the areas where extant iguanids are distributed. They have never been sympatric in North and South America nor in Madagascar. They could have co-occurred in Africa but the fossil record is too sparse to establish this point.

Lacertids may have caused the extinction of the Iguanidae where the two families overlapped.

COMPETITIVE EXPLANATIONS AND THE FOSSIL RECORD

Competitive explanations have traditionally been used by palaeontologists to account for the replacement of one group by another. In all cases, these explanations have been questioned by a closer study of the fossil record (Raup, 1982; Benton, 1983, 1987, 1996; Miller, 2000). For contrary opinions, see Miller & Sepkoski (1988) and Sepkoski (1996).

Two taxa are said to be in competition if an increase in abundance by either one harms the other (MacArthur, 1972). Such competitive interactions are viewed as necessary correlates of evolution by natural selection, according to the idea clearly expressed by Darwin when he made an analogy between the number of species on the Earth and a surface entirely covered with "ten-thousand sharp wedges". In this metaphor, he stated that the origination of a new taxon can occur only by the displacement of a preexisting one.

There are several ways in which clade A replaces clade B in the fossil record, but two broad patterns emerges: the first is the competitive pattern and it would be like a pair of matched wedge-shaped clades, one decreasing and the other increasing side by side, best known as the double-wedge pattern. The second pattern has been called the "mass-extinction" replacement and it would show one group coming to an end abruptly and the other increasing thereafter (Benton, 1996).

The classic example of supposed long-term competitive interaction between brachiopods and bivalves was studied by Gould & Calloway (1980) and they find no evidence of competitive replacement. Instead, the data suggest a mass-extinction and opportunistic replacement pattern.

Three principles guide the analysis: first, postulated competitors should have met each other in at least some part of their ranges (evidence for shared stratigraphic and geographic distributions). We do know that lacertids and iguanids were sympatric

in the European Eocene, more than fifteen localities have yielded both iguanid and lacertid remains. Second, it is necessary to show that they shared some major aspects of their modes of life (as a proxy for a more precise demonstration that they shared a limiting ressource or a common enemy). Third, the reality of competitive replacement should be distinguishable in the fossil record by assessing the relative abundances of the two groups in question through time: the "double wedge" pattern.

MODE OF LIFE

Diet

It has been suggested that there is a fairly tight correlation between diet and crown shape in lizards (Hotton, 1955; Montanucci, 1968). However, on a broad scale, there appears to be little diet-related variation in crown form and the vast majority of pleurodont squamates have numerous, relatively small, unicuspid to tricuspid teeth. These tooth forms are associated with a variety of invertebrate prey types of food (arthropod-insect eating lizards) as well as some percentage of plant food. Fossil iguanids and lacertids presented such dental shapes (uni-, bi- or tricuspid teeth for lacertids; uni-tricuspid teeth for iguanids) and

they are both considered as generalized lizards or arthropod eaters.

Size

Competitive interactions between two groups imply that both taxa shared comparable body size. There are no body mass estimation techniques for fossil lizards. Here dentary size has been used as an estimate of size in fossil lizard taxa. The distribution of body size is right-skewed on untransformed axes (Fig.9). The tail of small numbers of large species is marked, and the smallest size class is not the most speciose. Recent examinations of the size distributions of mammals and birds support the notion that most species tend to be of intermediate size (Blackburn & Gaston, 1994; Fenchel, 1993). The right-skewed body size distribution of Eocene iguanid and lacertid lizards conforms to many vertebrate assembly studied, principally in North America (Brown & Nicoletto, 1991; Brown *et al.*, 1993; Maurer *et al.*, 1992; Gaston & Blackburn, 2000). Thus, this distribution is unlikely to be severely biased. The bar chart shows that Eocene iguanid and lacertid lizards shared comparable body size in Europe. A statistical test confirms this opinion. The Kolmogorov-Smirnov test (K-S) compares the complete shapes and positions of two distributions. The K-S test does not assume a normal distribution, and is then a suitable method for comparing the two samples (Hammer & Harper, 2006).
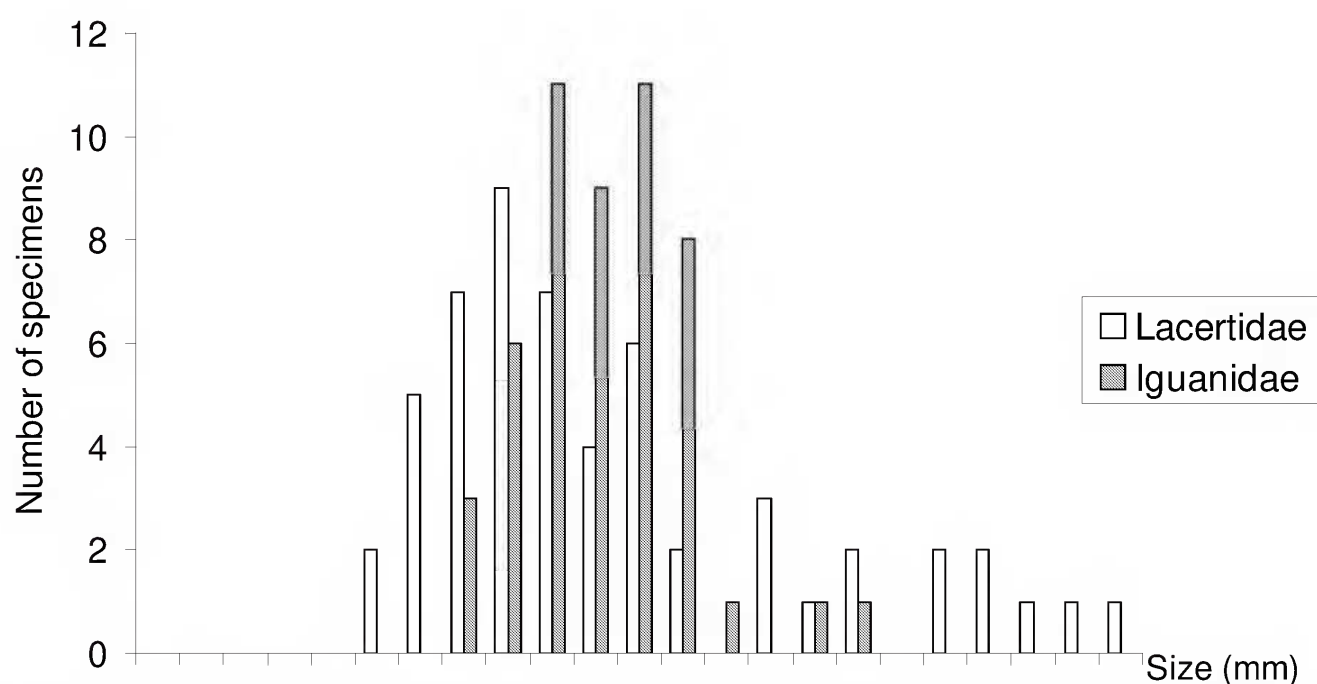

Fig.9- Size (measurements taken from the dentary) of the iguanid and lacertid lizards during the Eocene in Europe.

Using the K-S test, we arrive at the test statistic D = 0.24 and the probability of the equality of the two distributions is p = 0.076. Hence, the null hypothesis of equal distributions cannot be rejected.

DID LACERTID LIZARDS INCREASE IN DIVERSITY AT THE EXPENSE OF IGUANIDS?

Our raw data are the total number of iguanids and lacertids species and individuals living at any time during each of the mammalian standard level (MP) intervals in Europe.

Plots of number of species, or of individual animals, against time show that there is no evidence for double-wedge pattern in the fossil record (Fig.10). Instead, the general impression is one of positive association between iguanid and lacertid diversity, at least during the late Eocene.

The disappearance of iguanid lizards in Europe was associated with a single event: the Eocene-Oligocene extinction which deeply and permanently reduced the diversity of iguanids but only temporarily reduced the diversity of lacertids. The data suggest a mass-extinction replacement pattern.

In summary we find no evidence at all for the claim of negative interaction in diversity between iguanids and lacertids through time.

DISCUSSION AND CONCLUSION

A major turnover occurred in the european mammalian fauna near the Eocene-Oligocene (E-O) boundary (known as the Grande Coupure, see STEHLIN, 1909). Together with mammals, the Quercy localities contain an important assemblage of lizards. Their study has revealed an important change among lizards (RAGE, 1984; 1986; RAGE & AUGÉ, 1993; AUGÉ, 1993, 2000; MILNER *et al.*, 2000; DELFINO *et*

al., 2001). In Europe, the Late Eocene-Early Oligocene epochs constituted the most critical turning point in the Cenozoic history of the lizards.

During the Late Eocene, the lizard faunas were abundant and diverse. Nine families and 17 species are present in the standard level MP19 (mammalian standard level of Escamps), before the Eocene-Oligocene transition. Unfortunately, no lizard remains are known from the last Eocene standard level (MP20).

At the family and species levels, the lizards were severely affected by the "Grande Coupure". A drop in diversity is protracted between the MP20 (latest Eocene) and the MP21 levels (earliest Oligocene) and a low in diversity appears in the level MP21 (five families, eight species). Four families or subfamilies encountered in the European Late Eocene became extinct between the MP19-20/MP21 standard levels interval (Iguanidae, Gekkonidae, Glyptosaurinae, and Helodermatidae).
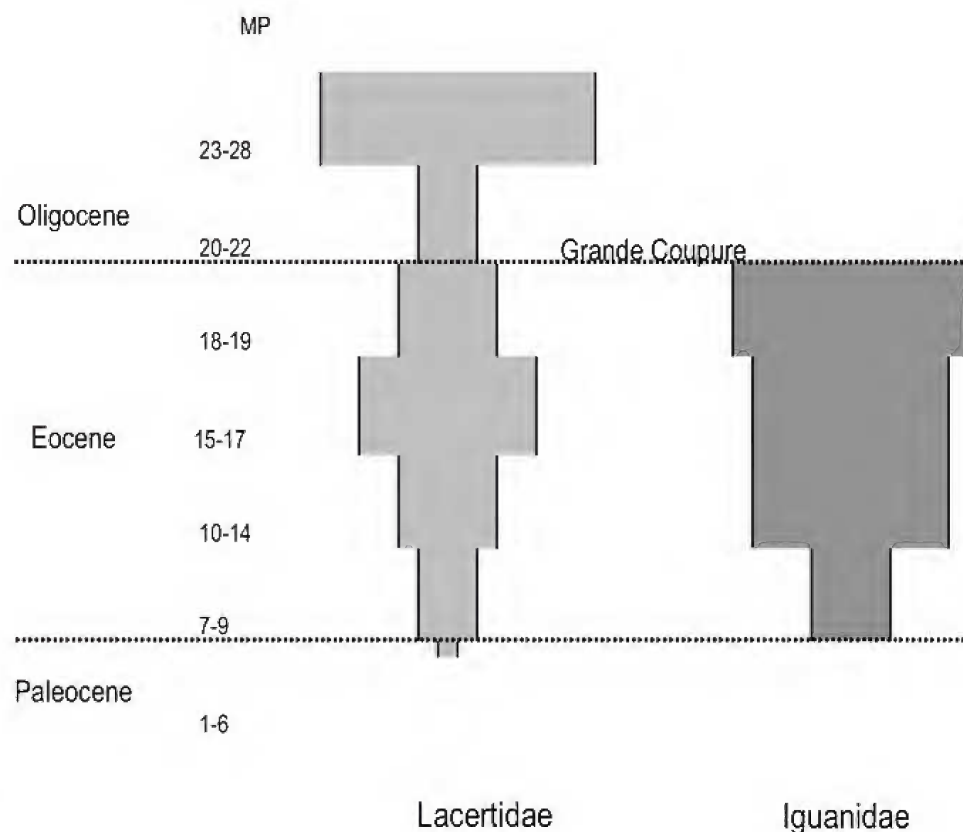

Fig.10- Relative diversity of iguanid and lacertid lizards through the Eocene and Oligocene in Europe. Time is standard level number, beginning in the early Eocene. The sole localities that have yielded both iguanid and lacertid lizards, are considered. *Eolacerta robusta* has not been included in the study, according to MÜLLER (2001), the suggestion that *Eolacerta* belongs to the modern family Lacertidae cannot be corroborated.

At lower taxonomic levels, estimates of species level extinctions range as high as 80%. They include members of virtually all the families present in the late Eocene. Thus, the E-O event provides evidence of a high rate of extinction not matched with originations.

All of the iguanid species known in the Late Eocene became extinct across the Eocene-Oligocene boundary. Similarly, the diverse lacertid fauna became extinct in Europe near the E-O boundary. However, at the beginning of the Oligocene, several lacertid species appear, with *Lacerta filholi*, and the development of several amblyodont, *i.e.*, durophagous members of the family Lacertidae (*Mediolacerta, Pseudeumeces, Dracaenosaurus*). During that time, no iguanid lizard reappeared in Europe.

Hence, it seems that extinction rates were equal for iguanid and lacertid species across the Eocene-Oligocene boundary. JOHST & BRANDL (1997) assume that large environmental perturbations have similar effects on all species. However, some species are slower to recover while other have more opportunities for speciation and immigration. Net diversification rates seem to accelerate for lacertid lizards after the Eocene-Oligocene event. Views on biases in speciation and immigration during recovery intervals seem to be dominated by assumption and supposition, with empirical evidence being weak or absent (JABLONSKI, 2005). Maybe the Eocene-Oligocene faunal turnover create an opportunity to examine this mechanisms.

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